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Communities of metazoan parasites in seven sympatric skate species (Elasmobranchii, Rajidae) from the English Channel and Celtic Sea differing in conservation status

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Abstract

Elasmobranch populations are in steep decline mainly due to overfishing bycatch, but parasites may accelerate the collapse of vulnerable and/or highly parasitized species. We therefore studied metazoan parasites of Rajidae from the northeast Atlantic: vulnerable *Leucoraja fullonica*, near-threatened *Raja brachyura*, *Raja clavata*, *Raja microocellata* and *Raja undulata*, and least-concerned *Raja montagui* and *Leucoraja naevus*. Overall prevalence varied from 19% for *R. montagui* to 100% for *L. fullonica*. Parasite communities differed between skate species, and prevalence and abundance were higher for *L. fullonica*, *R. microocellata*, and *R. undulata*. We recorded 11 parasite taxa in the study: three nematodes, six cestodes, one monogenean, and one myxosporean. Whatever the skate species, the parasite component community comprised at least two nematode taxa among *Phocanema* spp., *Proleptus* sp. and *Anisakis simplex*. DNA-sequencing revealed that *Phocanema azarasi* and *Phocanema krabbei* both occurred in *R. microocellata* and *R. undulata*. *Phocanema* spp. was first recorded in *L. fullonica*, *L. naevus*, *R. microocellata*, *R. montagui*, and *R. undulata*, as *Proleptus* sp. in *L. fullonica*, and *A. simplex* in *L. fullonica* and *R. clavata*, *Rockcestus* sp. and *Nybelinia* sp. in *R. undulata*, and gill-myxosporeans on *L. fullonica*, *L. naevus*, *R. microocellata*, and *R. undulata*. The occurrence of 16 new host–parasite associations suggests potential environmental changes. Information provided by trophically transmitted helminths confirmed an opportunistic skate diet based on crustaceans and fish. We discuss results in terms of host fitness loss, bioindicator role of parasites, and anisakiasis risk. We recommend incorporating parasitology in research to improve elasmobranch conservation.

KEYWORDS

conservation status, biological indicators, metazoan parasites, Rajidae

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1 | INTRODUCTION

Elasmobranch populations are dramatically declining worldwide, mainly due to overfishing (species targeted by fisheries and/or landed as bycatch), which interacts with other environmental stressors (e.g., habitat loss and degradation, climate change, and pollution), but also in relation with the elasmobranch K-selected life history (Barousse et al., 2014; Dulvy et al., 2021; Martin, 2005; Sguotti et al., 2016; for reviews). Long time series on elasmobranchs, for instance in the northern Adriatic Sea, highlight that skates have experienced the most dramatic reduction compared to sharks and catsharks, both in catch-per-unit-effort and in landings (during 2008–2012, they represented only 2.4% of their value in 1945–1949) (Barousse et al., 2014). A similar decline in skate populations is observed in European Atlantic waters and the North Sea, leading to decline of some species and changes in species composition (Brander, 1981; Dulvy et al., 2000; Ellis et al., 2005; Marandel et al., 2019; Rogers & Ellis, 2000; Sguotti et al., 2016). Since 2009, a multispecies fishing quota on skates has been applied to the entire EU Atlantic waters, in combination with bans from commercial exploitation for some skate species as well as regional or local quotas at the species level (Marandel et al., 2019).

Among environmental stressors, metazoan parasites are ubiquitous and could play a key role by contributing to accelerate the collapse of some species, in particular the most vulnerable and/or the most parasitized (Timi & Poulin, 2020 for review). Indeed, parasites decrease host fitness (e.g., lower energy reserves and life traits) and increase host mortality risk (almost three times higher for infected hosts compared to uninfected) (Robar et al., 2010; McElroy & De Buron, 2014; Timi & Poulin, 2020 for reviews). More specifically, metazoan parasites such as cestodes, monogeneans, and nematodes can induce pathology in elasmobranchs (Benz and Bullard, 2004; Borucinska and Adams, 2013; Borucinska & Heger, 1999; McVicar, 1972). For instance, trypanorhynch plerocerci and Lecanicephalidea adults are associated with severe histopathological lesions in the ray species *Rhinoptera bonasus* and *Gymnura zonura* (Borucinska et al., 2013; Borucinska & Bullard, 2011). The tetraphyllids *Echeneibothrium* sp. and *Rockacestus piriei* bothridia are shown to severely damage the host mucosal surface of the skate *Leucoraja naevus* (McVicar, 1972), and according to Williams (1966), species of cestodes which are rare in elasmobranchs are often highly pathogenic. In the context of increasing biodiversity loss and elasmobranch decline, knowledge on metazoan parasites appears all the more crucial; not only because they induce host fitness loss, but because they can provide diverse information on hosts (e.g., diet, habitat, migrations, ontogenic shifts) and more broadly on ecosystems (e.g., free-living biodiversity, environmental conditions) (e.g., Catalano et al., 2014; De Buron et al., 2009; MacKenzie, 2002; Marcogliese, 2005; Hudson et al., 2006; Timi & Poulin, 2020 for reviews). Parasites also influence competitive and predatory outcomes as well as host responses to other environmental stresses, and thus constitute a confounding factor leading to biased interpretations if not accounted for (e.g., Timi & Poulin, 2020, for

review). Parasitological data can thus help to improve elasmobranch conservation and management, and reduce the gap in knowledge for data-deficient species; comparison is particularly interesting between host species differing IUCN status as in our study.

Despite their interest, data on skate parasitofauna are often fragmented and scarce, with coverage varying considerably between species (e.g., helminths, mainly tapeworms, in *Raja* species around the British Isles; e.g., Williams, 1964, 1966), intestinal helminths of *Leucoraja naevus* in British waters (McVicar, 1977), parasitofauna of *Raja clavata* from the west coast of Ireland (Henderson & Dunne, 1999), and metazoan parasites of five *Raja* species in northwest Spain (Álvarez et al., 2006; Sanmartín et al., 2000). Therefore, the online database started by Pollerspöck and Straube in June 2009 and expanded continuously on metazoan parasites recorded in each elasmobranch species with scientific references is a very useful and valuable tool for parasitological research (<https://www.shark-references.com/species/host-parasites-list>; Pollerspöck & Straube, 2023), although the lists provided may suffer from historical host misidentifications and taxonomic modifications to parasite names.

In this exploratory study, we recovered metazoan parasites occurring in seven sympatric skate species from different grounds in coastal waters of the English Channel and Celtic Sea, an important northeast Atlantic fishing ground. The species studied are among the most common Rajidae landed in fish auctions of this area (Stephan et al., 2023), and thus the most readily available. According to IUCN (2024, <https://www.iucnredlist.org>), their conservation status in Europe varies from the “vulnerable” *Leucoraja fullonica* at one extreme, the “near-threatened” species *Raja brachyura*, *Raja clavata*, *Raja microcellata*, and *Raja undulata*, followed by *Raja montagui* and *Leucoraja naevus* which, despite intense trawling pressure and lack of new information on trends, are classed as “least-concerned”. These skates are demersal opportunist predators, eating a variety of benthic invertebrates (crustaceans, mollusks, polychaetes) and teleosts, and are usually found on continental shelves and slopes in the northeast Atlantic (Ebert & Bizzarro, 2007; Ellis et al., 1996, 2012; Moura et al., 2008). Different proportions of food items and habitat preferences can limit the ecological overlap between skate species (Ebert & Bizzarro, 2007; Ellis et al., 2012, 2015; Martin et al., 2010; McCully & Walls, 2015). For instance, *L. fullonica* and *L. naevus* are offshore species more frequently found in deep waters, whereas the studied *Raja* species tend to be inshore and common in shallower coastal waters, including large estuaries, rias and bays (Ellis et al., 2012, 2015; Martin et al., 2010; McCully & Walls, 2015). One can expect that metazoan parasites could help to discriminate between some of these sympatric skate species and that constraints due to parasitism may differ between skate species, with potentially dramatic consequences depending on their conservation status. In this context, our aims were (i) to document the communities of metazoan parasites among seven closely-related species of Rajidae, a vulnerable group for which ecological data are often limited, and (ii) to test the potential indicative role of parasites on skate hosts (e.g., diet).

2 | MATERIALS AND METHODS

2.1 | Study sites and fish samplings

A total of 114 skates belonging to *Leucoraja fullonica* (Linnaeus, 1758) (9 individuals), *Leucoraja naevus* (Müller and Henle, 1841) (15), *Raja brachyura* Lafont, 1873 (21), *Raja clavata* Linnaeus, 1758 (20), *Raja microocellata* Montagu, 1818 (14), *Raja montagui* Fowler, 1910 (21), and *Raja undulata* Lacépède, 1802 (14) were obtained in commercial fisheries (Table 1). Captures occurred in the northeast Atlantic in four ICES areas, respectively VIId (Eastern Channel), VIle (Western Channel), VIIf (Bristol Channel), and VIIh (Celtic Sea) (Figure 1 and Table 1), and from January to December 2018 (95 individuals), in June 2019 (one *L. fullonica*, one *R. undulata*), in August 2019 (nine *R. microocellata*), and in February 2020 (one *L. fullonica*, six *L. naevus*, one *R. undulata*). Before we collected skates at the fish auctions hall, specimens were placed on ice by fishermen or auction agents, and stored this way for one to several days. Immediately after their arrival at the laboratory, all the skates were frozen at -20°C .

2.2 | Fish measurements and parasitological research

After defrosting the skates, we measured their total length (TL in cm) and total mass (TM in g), then we determined the sex and assessed the immaturity/maturity stage according to ICES (2013). Mean TL and TM (with ranges) are provided for each skate species in Table 1.

We searched for metazoan parasites as follows. We removed and meticulously dissected under a binocular stereomicroscope the following fish organs: eyes, gills (each scrutinized separately), heart, digestive tract, and liver. Skin and body cavity were also carefully scrutinized. The digestive tract was opened longitudinally and divided into esophagus, stomach, and spiral intestine; we examined each of the seven internal folds under light stereomicroscope. Gills and eyes were not available for eight specimens among 21 *R. brachyura* and 12 among 14 *R. undulata* for which we could obtain only the viscera from the fishermen. All the 994 metazoan parasites found were cleaned in distilled water and numbered per organ/tissue and per fish.

TABLE 1 Number of skates (immatures/adults, females/males) belonging to seven species of Rajidae sampled in ICES zones of English Channel and Celtic Sea, with mean total length (TL, cm) and total mass (TM, g), range in parenthesis.

Rajidae	Abbreviation	ICES zone	Immatures		Adults		TL \pm CI (range)	TM \pm CI (range)
			Females	Males	Females	Males		
<i>Leucoraja fullonica</i>	Lful	7e, 7f, 7h	2	3	2	2	85 \pm 12 (61–106)	3242 \pm 1371 (1131–6410)
<i>Leucoraja naevus</i>	Lnae	7e, 7h	6	9	0	0	53 \pm 1 (50–56)	873 \pm 48 (760–1030)
<i>Raja brachyura</i>	Rbra	7d, 7e, 7f, 7h	11	9	1	0	68 \pm 9 (42–106)	3210 \pm 1431 (540–11,280)
<i>Raja clavata</i>	Rcla	7d, 7e	10	9	1	0	73 \pm 5 (52–96)	2801 \pm 685 (806–6110)
<i>Raja microocellata</i>	Rmic	7e, 7f	7	2	3	2	71 \pm 5 (56–84)	2695 \pm 665 (1110–4819)
<i>Raja montagui</i>	Rmon	7d, 7e, 7f	8	8	3	2	54 \pm 3 (44–69)	974 \pm 247 (495–2566)
<i>Raja undulata</i>	Rund	7e	2	4	4	4	80 \pm 2 (61–94)	3245 \pm 193 (1480–4680)

Abbreviation: CI = confidence interval (95%).

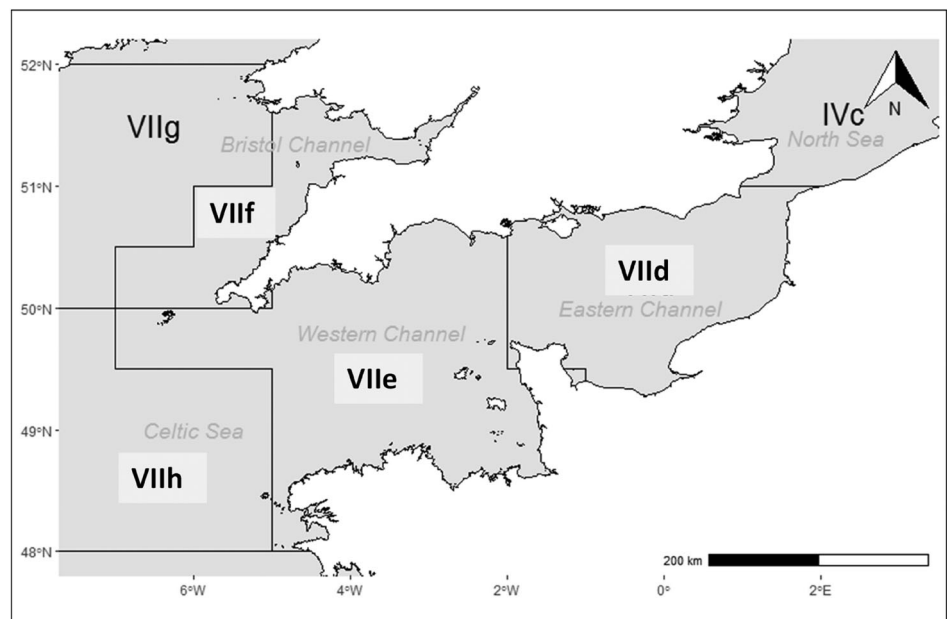


FIGURE 1 Geographical position of the four ICES areas in the northeast Atlantic where the seven species of Rajidae were caught: VIId (Eastern Channel), VIle (Western Channel), VIIf (Bristol Channel), and VIIh (Celtic Sea).

Then, each parasite was morphologically identified to the lowest taxonomic level possible under a light microscope, both immediately when found (just defrosted) and later after fixation in 70% ethanol. Drawings with camera lucida and photographs were made for some specimens of helminths prepared as whole mounts between a glass slide and a slip cover. Morphological identification referred to Price (1942) for Monogenea; Euzet (1956), Khalil et al. (1994), Palm (1999), Palm and Walter (2000), Beveridge and Campbell (2007), and Caira et al. (2021) for Cestoda; Moravec et al. (2002), Anderson et al. (2009), and Bao et al. (2023) for Nematoda; and Lom and Dyková (2006) for Myxozoa. Some nematode specimens (i.e., *Anisakis simplex*, *Phocanema* spp. and *Proleptus* sp.) were preserved in 95% ethanol for molecular identification to validate morphological identification (see below).

The parasitological parameters used to describe the parasite community structure were prevalence (P, number of skates infected with a particular parasite taxon divided by the number of skates examined), taxa richness (number of parasite taxa infecting a host species), and abundance (A, number of individuals of a particular parasite taxon in/on a single skate regardless of whether or not the skate is infected) (Bush et al., 1997). In the cases of *Echeneibothrium*, *Nybelinia* and *Onchobothrium*, parasitological parameters were calculated based on genera. Indeed, due to the generally high specificity of Cestoda for their definitive host (Caira & Jensen, 2014 for review), we considered that these three cestodes we recorded in several skate species corresponded to several parasite species (one per skate host species).

2.3 | Molecular identification of nematodes via DNA sequencing

A total of 27 nematodes among 551 recorded in the study were DNA-sequenced, and 20 specimens were successfully identified. The DNA of each individual parasite was extracted using Wizard[®] Genomic DNA Purification Kit (Promega) following the manufacturer's instructions after grinding the parasite with a sterile piston pellet. DNA was kept at -20°C until used. The 18S rDNA partial gene (18S) was amplified using the primers 18SF (5'-CGCGAATRGCTCATTACAACAGC-3') and 18SR (5'-GGCGGTATCTGATCGCC-3') as described in Floyd et al. (2005), with an initial denaturation of 15 min at 95°C , 40 cycles of 94°C for 30 s, 55°C for 40 s, and 68°C for 1 min 30 s, and a final elongation step of 10 min at 68°C . The mitochondrial cytochrome c oxidase subunit II (cox2) gene was amplified using the primers 211 F (5'-TTT TCT AGT TAT ATA GAT TGR TTY AT-3') and 210 R (5'-CAC CAA CTC TTA AAA TTA TC-3') (Nadler & Hudspeth, 2000) with an initial denaturation of 3 min at 94°C followed by 34 cycles at 94°C for 30 s, 46°C for 60 s, and 72°C for 90 s prior to post amplification at 72°C for 10 min (Valentini et al., 2006).

Automated DNA sequencing was performed by Genoscreen, and then sequences were analyzed using BioEdit software to obtain consensus sequences from forward and reverse sequences. They were subsequently compared with available 18S or Cox2 sequences of nematode species by GenBank Blast software (Basic Local Alignment Search Tool) in March 2023 (Altschul et al., 1997).

2.4 | Statistical analyses

Throughout the following sections, data are reported as means followed by 95% confidence interval (CI). For prevalence, the 95% CI was calculated using the score method (Newcombe, 1998). All statistical analyses were performed with R software v. 4.0.2 (R Core Team, 2020).

Prevalence was compared between skate species using a likelihood ratio test applied to a generalized linear model (distribution: binomial, link function: logit) [R package 'car' (Fox & Weisberg, 2019)]. Models were built for the total prevalence (i.e., all parasite taxa confounded), prevalence of all trophically transmitted parasites confounded, and prevalence of each individual parasite taxon. Pairwise comparisons of estimated marginal means (EMMeans) were subsequently performed using the 'emmeans' R package (Lenth, 2021), with p values adjusted using the false discovery rate correction (Benjamini & Hochberg, 1995). The same approach was used to analyze abundance data except that models were built using a quasi-Poisson distribution (link function: log) and F tests were performed.

3 | RESULTS

3.1 | Metazoan parasites found in Rajidae

In total, 51% (CI 42–60%) of the skates harbored one to four taxa of metazoan parasites, with a taxa richness of 0.8 ± 0.2 parasite taxa per individual and an abundance of 8.7 ± 4.5 parasites per individual (Tables 2 and 3). According to morphological identification, 11 parasite taxa occurred in the whole sampling of skates: one Myxosporea (unidentified) and one Monogenea (*Rajonchocotyle emarginata*) on gills, and six Cestoda (*Grillotia erinaceus*, *Tritaphros retzii*, and the genera *Echeneibothrium*, *Nybelinia*, *Onchobothrium*, and *Rockcestus*) and three Nematoda (*Anisakis simplex*, and the genera *Phocanema* and *Proleptus*), all trophically transmitted (Table 2). Based on DNA-sequencing made on 27 isolated nematodes from skates, 20 individuals were molecularly identified, i.e., seven *Phocanema krabbei*, five *Proleptus* sp., four *Phocanema azarasi*, and four *Anisakis simplex* s.s. (Table 4). All sequences had an identity percentage with sequences present in the National Center for Biological Information database above 99%, and percentage of coverage was always at least 99% for all sequences (Table 4). All the sequences generated in this study were deposited in GenBank.

A total of 16 new host–parasite associations are documented in Table 2 (in bold).

Parasites were mainly recorded in the digestive tract (38% of the skates, CI 29–47%), then in the body cavity (23%, CI 16–31%) and to a lesser extent on the gills (11%, CI 6–18%). No infections were found in the other organs examined (eyes, skin, heart, and liver).

Trophically transmitted (vs gill) parasites were largely dominant, with prevalence and abundance of 48% (CI 39–57%) and 5.8 ± 2.4 parasites per skate individual, respectively. Among trophically

TABLE 2 Prevalence (P%, CI) and abundance (A ± CI) of metazoan parasites in seven sympatric species of Rajidae (abbreviations in Table 1), with IUCN European status [Least-Concern (LC), Near-Threatened (NT), Vulnerable (Vu)] from English Channel and Celtic Sea, and for trophically-transmitted helminths (Pth% and Ath)

Rajidae	IUCN	N	Overall P% (CI)	Pth% (CI)	Overall A ± CI	Ath ± CI	Parasite taxa
<i>Lful</i>	Vu	9	100 (70–100) ^a	100 (70–100) ^a	29.7 ± 45.1 ^a	18.6 ± 19.9 ^a	Myxo, Nybe, Asim, Phoc, Prol
<i>Lnae</i>	LC	15	47 (25–70) ^{bc}	33 (15–58) ^c	7.6 ± 9.8 ^a	0.9 ± 0.8 ^b	Myxo, Rema, Eche, Geri, Asim, Phoc
<i>Rbra</i>	NT	21	29 (14–47) ^c	29 (14–47) ^c	0.8 ± 1.0 ^b	0.8 ± 1.0 ^b	Geri, Asim, Prol
<i>Rcla</i>	NT	20	40 (22–61) ^c	40 (22–61) ^c	1.9 ± 1.8 ^b	1.9 ± 1.8 ^b	Eche, Tret, Asim, Prol
<i>Rmic</i>	NT	14	93 (69–99) ^a	93 (69–99) ^a	28.3 ± 22.9 ^a	19.3 ± 10.6 ^a	Myxo, Eche, Onch, Asim, Phoc, † Prol
<i>Rmon</i>	LC	21	19 (8–40) ^c	19 (8–40) ^c	1.3 ± 1.6 ^b	1.3 ± 1.6 ^b	Eche, Phoc, Prol
<i>Rund</i>	NT	14	79 (52–92) ^{ab}	71 (42–60) ^b	9.7 ± 6.9 ^a	9.4 ± 7.0 ^a	Myxo, Nybe, Onch, Rock, Phoc[†]

Note: Parasite taxa: Myxosporea (Myxo), *Rajonchocotyle emarginata* (Rema), *Echeneibothrium* spp. (Eche), *Grillotia erinaceus* (Geri), *Nybelinia* spp. (Nybe), *Onchobothrium* spp. (Onch), *Rockacestus* sp. (Rock), *Tritaphros retzii* (Tret), *Anisakis simplex* (Asim), *Phocanema* spp. (Phoc), *Proleptus* sp. (Prol). First records of parasites in bold. N = sample size, CI = confidence interval (95%). Due to the generally high specificity of Cestoda for their definitive host (Caira and Jensen, 2014 for review), we considered that Eche, Nybe and Onch recorded in several skate species in our study corresponded to several parasite species (one per skate host species). Different letters indicated statistical differences between skate species for each parasitological parameter.

[†]Both *Phocanema azarasi* and *Phocanema krabbei* molecularly identified and recorded for the first time.

TABLE 3 Metazoan parasites found in skates belonging to seven species of Rajidae: microhabitat (MH), total prevalence (P%, CI), abundance (A ± CI), maximum number of parasites (Max A) and infections pathways according to Dogiel et al. (1961), Williams (1966), Whittington and Kearns (1986), Palm and Walter (2000), Lom and Dyková (2006), Beveridge and Campbell (2007), Moravec (2007), Tedesco et al. (2020), Caira et al. (2023)

Parasite taxa	MH	P% (CI)	A ± CI	Max A	Infection pathways
Myxozoa					
Myxosporea	G	9.6 (6.7–19.8)	3.52 ± 3.29	100	Random contact with spores
Monogenea					
<i>Rajonchocotyle emarginata</i>	G	1.1 (0.2–5.8)	0.01 ± 0.02	1	Active attachment on gill lamellae
Cestoda					
<i>Echeneibothrium</i> spp.	SV	7.9 (4.2–14.3)	0.30 ± 0.29	15	Ingestion of crustaceans, teleosts (Hi2, Hp)
<i>Grillotia erinaceus</i>	ES, SV	3.5 (1.4–8.7)	0.04 ± 0.05	2	Ingestion of teleosts (Hi2)
<i>Nybelinia</i> spp.	ES, SV	7.9 (4.2–14.3)	0.46 ± 0.43	20	Ingestion of cephalopods, fish (Hi2)
<i>Onchobothrium</i> spp.	SV	7.9 (4.2–14.3)	0.15 ± 0.11	4	Ingestion of crustaceans, cephalopods, fish (Hi2, Hp)
<i>Rockacestus</i> sp.	SV	0.9 (0.2–4.8)	0.01 ± 0.02	1	Ingestion of benthic invertebrates, fish (Hi2, Hp)
<i>Tritaphros retzii</i>	SV	0.9 (0.2–4.8)	0.01 ± 0.02	1	Ingestion of teleosts (Hi2)
Nematoda					
<i>Anisakis simplex</i>	BC, SV	9.6 (5.5–16.5)	1.05 ± 1.05	55	Ingestion of crustaceans, cephalopods, fish (Hi, Hp)
<i>Phocanema</i> spp. ^a	BC	18.4 (12.4–26.5)	3.04 ± 1.67	56	Ingestion of crustaceans, cephalopods, fish (Hi, Hp)
<i>Proleptus</i> sp.	ES	14.0 (8.8–21.6)	0.74 ± 0.61	30	Ingestion of decapods (Hi)

Abbreviations: BC, body cavity; CI, confidence interval (95%); ES, esophagous and stomach; G, gills; Hd, definitive host; Hi, intermediate host; Hp, paratenic host; SV, spiral valve.

^aTwo species of *Phocanema* were molecularly identified (*P. azarasi* and *P. krabbei*).

transmitted parasites, nematodes were the most prevalent infecting 37% (CI 29–46%) of the skates with an abundance of 1.6 ± 1.2 parasites per individual, followed by cestodes for which total prevalence and abundance were, respectively, 25% (CI 18–33%) and 0.2 ± 0.2 parasite per individual. The dominant taxa of metazoan parasites were, in decreasing order, the nematodes *Phocanema* spp., *Proleptus* sp., and *Anisakis simplex*, each taxon being encountered in five of the seven skate species (Tables 2 and 3).

3.2 | Differences in parasitism between the seven sympatric species of Rajidae

Overall prevalence and abundance of metazoan parasites differed significantly among skate species (prevalence: $\chi^2 = 43.02$, $df = 6$, $p < 0.001$; abundance: $\chi^2 = 54.68$, $df = 6$, $p < 0.001$), as well as when considering only trophically transmitted helminths (prevalence: $\chi^2 = 43.02$, $df = 6$, $p < 0.001$; abundance: $\chi^2 = 61.21$, $df = 6$,

TABLE 4 Molecular identification of 20 nematodes from skates: comparison of COX2 and 18S sequences with previously published data in GenBank

Present study samples			BLAST results					
Sequence	GenBank reference	Length	Target	Identification	GenBank reference	Identity percentage	Query coverage	Reference
Lf2-BC-01	PP926494	422	COX2	<i>Anisakis simplex</i>	MN961158.1	100%	100%	Pons-Bordas et al. 2020
Lf2-BC-02	PP926495	422	COX2	<i>Anisakis simplex</i>	MN961171.1	100%	100%	Pons-Bordas et al. 2020
Lf2-BC04	PP926496	422	COX2	<i>Anisakis simplex</i>	KT852534.1	100%	100%	Klapper et al. 2016
Lf2-SV-01	PP926497	422	COX2	<i>Anisakis simplex</i>	LT883293.1	100%	100%	
Rb56-ES-01	OR515670	650	18S	<i>Proleptus</i> sp.	JF934733.1	99.69%	100%	Laetsch et al. 2012
Rb56-ES-02	OR515671	650	18S	<i>Proleptus</i> sp.	JF934733.1	99.69%	100%	Laetsch et al. 2012
Rb56-ES-05	OR515672	650	18S	<i>Proleptus</i> sp.	JF934733.1	99.69%	100%	Laetsch et al. 2012
Rb56-ES-06	OR515673	650	18S	<i>Proleptus</i> sp.	JF934733.1	99.69%	100%	Laetsch et al. 2012
Rb56-ES-07	OR515674	650	18S	<i>Proleptus</i> sp.	JF934733.1	99.69%	100%	Laetsch et al. 2012
Rm3-BC-01	PP911372	425	COX2	<i>Pseudoterranova krabbei</i> ^a	HM147279.1	99.06%	99%	
Rm3-BC-02	PP911367	425	COX2	<i>Pseudoterranova azarasi</i> ^a	NC_027163.1	100%	100%	Liu et al. 2015
Rm3-BC-03	PP911373	425	COX2	<i>Pseudoterranova krabbei</i> ^a	HM147279.1	99.76%	99%	
Rm3-BC-04	PP911374	425	COX2	<i>Pseudoterranova krabbei</i> ^a	HM147279.1	99.76%	99%	
Rm3-BC-05	PP911375	425	COX2	<i>Pseudoterranova krabbei</i> ^a	HM147279.1	99.06%	99%	
Rm3-BC-06	PP911368	425	COX2	<i>Pseudoterranova azarasi</i> ^a	NC_027163.1	99.53%	100%	Liu et al. 2015
Ru2-BC-01	PP911369	425	COX2	<i>Pseudoterranova krabbei</i> ^a	HM147279.1	100%	99%	
Ru2-BC-02	PP911365	425	COX2	<i>Pseudoterranova azarasi</i> ^a	NC_027163.1	99.29%	100%	Liu et al. 2015
Ru2-BC-03	PP911370	425	COX2	<i>Pseudoterranova krabbei</i> ^a	HM147279.1	99.29%	99%	
Ru2-BC-04	PP911366	425	COX2	<i>Pseudoterranova azarasi</i> ^a	NC_027163.1	99.76%	100%	Liu et al. 2015
Ru2-BC-05	PP911371	425	COX2	<i>Pseudoterranova krabbei</i> ^a	HM147279.1	99.53%	99%	

Abbreviations: BC, body cavity; ES, esophagous and stomach; Lf, *Leucoraja fullonica*; Rb, *Raja brachyura*; Rm, *Raja microocellata*; Ru, *Raja undulata*; SV, spiral valve.

^aRecent taxonomical studies (Bao et al., 2023) separated the genus *Pseudoterranova* in two genera, *Phocanema* and *Pseudoterranova*. Thus, the individuals whose sequences matched with *Pseudoterranova azarasi* or *Pseudoterranova krabbei* in fact belong to the species *Phocanema azarasi* or *Phocanema krabbei*, respectively.

$p < 0.001$); *L. fullonica*, *R. microocellata*, and *R. undulata* were significantly more parasitized than the four other skate species (Table 2).

The composition of parasite communities varied between host species, with significant differences for both prevalence and abundance of *A. simplex* and *Phocanema* spp. and for abundance of *Proleptus* sp. (Tables 5 and 6). *L. fullonica* was more infected by

A. simplex in terms of prevalence and abundance and by *Proleptus* sp. in terms of abundance, whereas *R. microocellata* and to a lesser extent *R. undulata* were more infected by *Phocanema* spp. both in terms of prevalence and abundance (Figure 2). Each skate species was parasitized by at least two of the three nematode taxa, and whatever the skate species, the parasite component community was always dominated by nematodes (Table 5).

TABLE 5 Prevalence (P%, CI) and abundance (A ± CI) of metazoan parasite taxa in each species of Rajidae.

Parasite taxa	Lful		Lnae		Rbra ^a		Rcla		Rmic		Rmon		Rund ^a	
	P% (CI)	A ± CI	P% (CI)	A ± CI	P% (CI)	A ± CI	P% (CI)	A ± CI	P% (CI)	A ± CI	P% (CI)	A ± CI	P% (CI)	A ± CI
Myxo	11 (2–44)	11.1 ± 25.6	13 (4–38)	6.7 ± 9.7					36 (16–61)	9.0 ± 15.3			50 (9–91) ^a	2.5 ± 31.8 ^a
Rema			7 (1–30)	0.1 ± 0.1										
Rock														
Eche			7 (1–30)	0.3 ± 0.6			10 (3–30)	0.3 ± 0.5	29 (12–55)	0.4 ± 0.4	10 (3–29)	0.9 ± 1.5	7 (1–32)	0.1 ± 0.2
Geri			7 (1–30)	0.1 ± 0.3	14 (5–35)	0.1 ± 0.2								
Nybe	56 (5–35)	2.7 ± 2.8											29 (12–55)	2.1 ± 3.2
Onch									43 (21–67)	0.9 ± 0.8			21 (8–48)	0.3 ± 0.4
Tret							5 (1–24)	0.1 ± 0.1						
Asim	56 (5–35)	10.6 ± 13.7	20 (7–45)	0.4 ± 0.5	5 (1–23)	0.1 ± 0.1	5 (1–24)	0.6 ± 1.2	7 (1–31)	0.5 ± 1.1				
Phoc	11 (2–44)	0.1 ± 0.3	7 (1–30)	0.1 ± 0.1					79 (52–92)	17.4 ± 10.4	5 (1–23)	0.2 ± 0.5	50 (27–73)	6.9 ± 5.3
ProI	33 (12–65)	5.2 ± 7.9			19 (8–40)	0.6 ± 0.9	30 (15–52)	1.0 ± 0.9	7 (1–31)	0.1 ± 0.2	10 (3–29)	0.2 ± 0.3		

Note: Skate species and parasite taxa abbreviations given in Tables 1 and 2, CI = confidence interval (95%). Due to the generally high specificity of Cestoda for their definitive host (Caira & Jensen, 2014 for review), we considered that Eche, Nybe and Onch recorded in several skate species in our study corresponded to several parasite species (one per skate host species).

^aGills could not be examined for eight among 21 *R. brachyura* and 12 among 14 *R. undulata*.

Parasite taxa	Prevalence			Abundance		
	χ^2	df	p	F	df	p
Myxo	2.805	2	0.246	0.094	2	0.909
Eche	3.401	3	0.333	0.450	3	0.718
Geri	0.543	1	0.461	0.004	1	0.948
Nybe	1.672	1	0.196	0.076	1	0.785
Onch	1.495	1	0.221	2.835	1	0.104
Asim	13.203	4	0.010 (*)	9.653	4	<0.001 (***)
Phoc	31.984	4	<0.001 (***)	18.471	2	<0.001 (***)
Prol	5.465	4	0.242	5.775	4	<0.001 (***)

Note: Prevalence: likelihood ratio test applied on a generalized linear model with a binomial distribution and a logit link function. Abundance: F test applied on a generalized linear model with a quasi-Poisson distribution and a log link function. Abbreviations of parasite taxa given in Table 2.

TABLE 6 Statistical comparison between skate species for prevalences and abundances of metazoan parasite taxa.

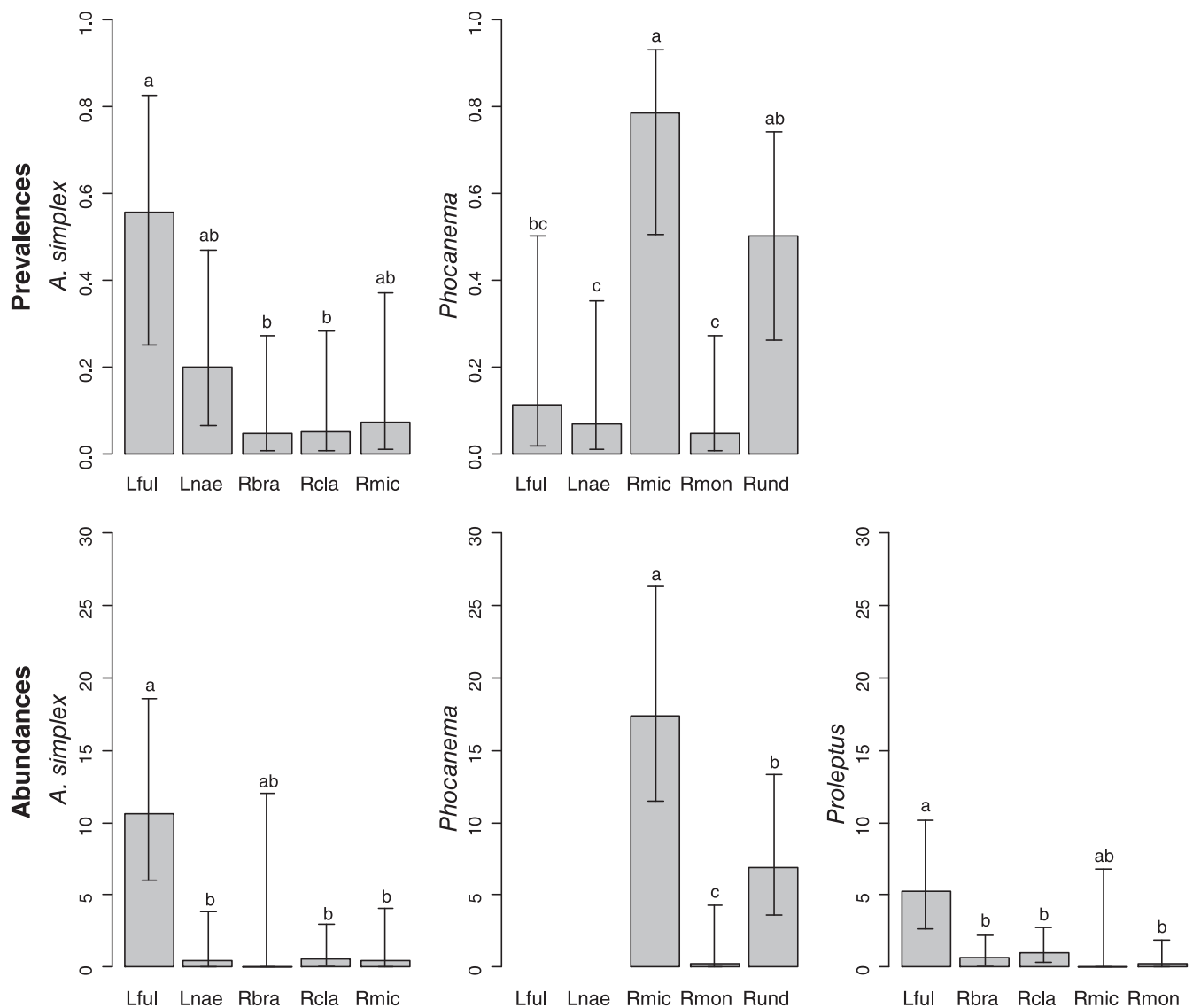


FIGURE 2 Mean prevalences (\pm CI) of *Anisakis simplex* and *Phocanema* spp., and mean abundances (\pm CI) of *A. simplex*, *Proleptus* sp., and *Phocanema* spp. in the seven species of Rajidae. Abbreviations of skate species are given in Table 1. Different letters indicated statistical differences between skate species for each parasitological parameter.

4 | DISCUSSION

4.1 | Parasite component communities of Rajidae and comparison with previous studies

Comparison with previous parasitological surveys (e.g., Álvarez et al., 2006; McVicar, 1977; Sanmartín et al., 2000) is difficult because of differences in methods (fish previously frozen before parasitological examination in our study vs. freshly euthanized), but also in sampling effort, areas, and timing that can at least partially account for some differences between the component communities of metazoan parasites. In particular, the freezing of skates before parasite research can partly explain why we found far fewer platyhelminths such as cestodes and monogeneans than in previous surveys. Indeed, these soft-bodied helminths can be damaged or even destroyed by the ice crystals formed during freezing, in contrast to nematodes that are highly resistant to freezing due to their protective outer cuticle and were dominant in our study. However, despite research on defrosted skates and relatively low sampling size, our exploratory study revealed 16 new host–parasite associations in Rajidae from the English Channel and Celtic Sea, among them 10 involving nematodes (Table 2).

In the case of *L. fullonica*, despite the lack of a specific parasitological study and other data on prevalences, at least 11 species among them eight platyhelminths were registered according to the online bibliographical database of Pollerspöck and Straube (2023) and Williams (1964), versus five in our study, among them four new records, i.e., the three nematode taxa (*A. simplex*, *Phocanema* spp., and *Proleptus* sp.) and an unidentified gill myxosporean. Concerning *L. naevus*, 19 species of metazoan parasites were listed by Pollerspöck and Straube (2023), and 14 parasite taxa of which eight platyhelminths occurred with a prevalence of 100% in the 263 *L. naevus* studied by McVicar (1977) in British waters including the English Channel, whereas 47% of our 14 specimens were infected by six taxa. Among them, only two cestodes, *Echeneibothrium* spp. and *Grillotia erinaceus*, were in common; *A. simplex*, previously considered accidental, was the most prevalent species in our study, and we recorded *Phocanema* spp. for the first time in *L. naevus*. Note that recent taxonomical studies by Bao et al. (2023) have resulted in the resurrection of the genus *Phocanema*, previously included in the genus *Pseudoterranova*. On the northwest coast of Spain, both *Raja brachyura* (60 individuals) and *Raja microocellata* (52) harbored 18 parasite taxa with prevalences up to 92% and 96%, respectively (Álvarez et al., 2006), versus respectively three and seven taxa in *R. brachyura* (21 individuals) and *R. microocellata* (14) in our study in the northeast Atlantic with overall prevalences of 29% and 93%. *Phocanema azarasi*, *Phocanema krabbei* and an unidentified gill myxosporean were registered for the first time in *R. microocellata*; no new records occurred for *R. brachyura*. Note that 28 and 24 species of metazoan parasites, respectively, were listed in *R. brachyura* and *R. microocellata* by Pollerspöck and Straube (2023). Concerning *Raja undulata*, among the 17 parasite species enumerated by Pollerspöck and Straube (2023), 16 were recorded with a total prevalence of 99% in 78 individuals from the northwest coast of Spain (Álvarez et al., 2006; Sanmartín et al., 2000). Among them, only

the cestode *Onchobothrium* spp. was found in our 14 *R. undulata* studied, of which 79% were parasitized. In total, we detected six parasite taxa in *R. undulata*, including five new records, i.e., *P. azarasi* and *P. krabbei*, the cestodes *Rockacestus* sp. and *Nybelinia* spp., and an unidentified gill myxosporean. Parasite diversity was also higher in the six Spanish *R. montagui* studied by Álvarez et al. (2006) harboring seven parasite taxa (prevalence not available), compared to our 21 specimens from the northeast Atlantic parasitized with a total prevalence of 19% by three taxa, including the new record of *Phocanema* spp. According to Pollerspöck and Straube (2023), 22 species of metazoan parasites have been registered in *R. montagui*. For *R. clavata*, despite 71 parasite species listed by Pollerspöck and Straube (2023) (even if all of these are probably not valid), only four taxa were recorded in the 28 skates from the west coast of Ireland studied by Henderson and Dunne (1999) as in our 20 individuals. *Proleptus* sp. was the single parasite taxon recorded in both studies with respective prevalences of 21% and 30%. Interestingly, no cestodes occurred in Irish *R. clavata* (Henderson & Dunne, 1999), despite at least 27 species mentioned in the database of Pollerspöck and Straube (2023). In addition to *Proleptus* sp., we found two cestode species, *Echeneibothrium* spp. and *Tri-taphros retzii*, in *R. clavata*, and *A. simplex* recorded for the first time.

Notwithstanding the fact that we recorded 16 new host–parasite associations, the parasite communities we described in skates from the English Channel and Celtic Sea appeared depauperate. As previously evoked, this could be partially explained by the possible loss of soft-bodied helminths due to freezing and our lower sampling effort, but it could also reflect environmental changes over time, encompassing a potential decrease of free-living biodiversity affecting heteroxenous parasites such as trophically transmitted helminths (e.g., Hatcher et al., 2012; Hudson et al., 2006; Marcogliese, 2005; Timi & Poulin, 2020 for reviews). Intensive fishing can drive declines in fish parasite diversity, especially trophically transmitted parasites that require multiple host species, some of which are the top predators most sensitive to fishing impacts (Wood et al., 2014). In this way, MacKenzie & Pert (2018) showed evidence for the decline and possible extinction of a digenean parasite species caused by intensive fishing of the near-threatened *Raja clavata*, suggesting that the population size of the final host was below the threshold required for successful transmission of the parasite. Differences between parasite component communities can also originate from differences in sampling areas potentially inhabited by different intermediate, paratenic, and/or definitive host species, as observed for *R. undulata* between the continental shelf and the estuary of Muros–Noia in northwest Spain (Álvarez et al., 2006; Sanmartín et al., 2000). Our record of 16 new host–parasite associations involving Rajidae may also result from modifications of both abiotic conditions and biocenoses in the context of global change. Indeed, water temperatures in the English Channel and Celtic Sea have increased 0.17–0.45°C per decade between 1985 and 2014, with consequences on free-living species from plankton to seabirds (Hughes et al., 2017; Lauria et al., 2013). Moreover, the occurrence of both *Phocanema* spp., the dominant parasite taxon of our study and firstly recorded in Rajidae (i.e., *L. fullonica*, *L. naevus*, *R. microocellata*, *R. montagui*, and *R. undulata*), and

TABLE 7 Bibliographical data on diet composition (%) of Rajidae species according to Moura et al. (2008) for *Raja undulata* and to Ebert and Bizzarro (2007) for the other skate species.

Rajidae	Fish	Decapods	Other crustaceans	Cephalopods	Other mollusks	Polychetes
<i>Leucoraja fullonica</i>	65.46	22.15	6.82	4.37	0	1.20
<i>Leucoraja naevus</i>	45.57	20.31	19.17	2.05	0.59	12.19
<i>Raja brachyura</i>	34.32	25.58	35.13	0.37	1.29	3.31
<i>Raja clavata</i>	21.03	55.37	14.02	3.45	2.75	3.37
<i>Raja microocellata</i>	49.21	46.39	1.69	0.76	0.21	1.73
<i>Raja montagui</i>	6.17	65.11	17.83	0.28	0.45	10.03
<i>Raja undulata</i>	7.90	91.64	0	0.14	0.01	0

A. simplex, newly recorded in *L. fullonica* and *R. clavata*, may confirm the increase of anisakiasis observed worldwide (Fiorenza et al., 2020; Mattiucci et al., 2017). It raises the question of anisakiasis risk for human consumption, as the genera most often associated with anisakiasis are *Anisakis* and *Pseudoterranova* (Chai et al., 2005 for review), the latter now divided in two distinct genera, *Pseudoterranova* and *Phocanema* (Bao et al., 2023).

4.2 | Information on skates provided by metazoan parasites and potential use as bioindicators

Nematodes and cestodes, the main taxa found in the skates from our study and in the database of Pollerspöck and Straube (2023), are trophically transmitted, and thus can provide information on prey ingested by skate hosts. Data on host diet can also give information on the life cycle of parasites. The parasitism patterns we observed (Table 5) corroborated resemblances in the diet composition between the seven sympatric skate species studied, based on fish and crustaceans (in particular decapods), and to a lesser extent cephalopods (Ebert & Bizzarro, 2007; Moura et al. (2008), see bibliographical data in Table 7). All these prey are intermediate and/or paratenic hosts of the nematodes and cestodes we recorded here (Table 3). Moreover, differences in the parasitism patterns of trophically transmitted helminths may indicate prey preferences, i.e., the most abundantly and/or frequently ingested. For instance, the main parasite taxa recorded in *L. fullonica*, including the most prevalent and abundant *A. simplex* (56%, 10.6 ± 13.7), are transmitted by the main food items, i.e., fish, crustaceans, and cephalopods in decreasing order (Ebert & Bizzarro, 2007; Table 7). Nevertheless, the relatively high prevalence and abundance of *Proleptus* sp. (33%, 5.2 ± 7.9) in *L. fullonica* also highlight the importance of intermediate host decapods in the diet of this skate species.

Differences in diet, foraging, and/or habitat use can occur depending on age and between sexes, as demonstrated for the seven Rajidae species studied (Bisch et al., 2022; Farias et al., 2006; Moura et al., 2008), with consequences on parasitism patterns. Therefore, further investigations are needed to obtain extensive data on skates varying in age and sex, and then allowing the use of parasites as

bioindicators of feeding ecology and ontogenic dietary shifts of skate species (MacKenzie, 2002).

4.3 | Metazoan parasites as environmental stressors potentially contributing to the collapse of some Rajidae

Parasites increase host mortality risk (e.g., Robar et al., 2010; Timi & Poulin, 2020) and cause anything from undetectable to drastic changes in host fitness (Poulin, 1998). Severe pathogen effects observed in elasmobranchs including Rajidae have been associated with the occurrence of parasitic helminths (nematodes, cestodes, and monogeneans), probably resulting in decreased host condition (McVicar, 1972; Borucinska & Heger, 1999; Borucinska and Adams, 2013). In our study, the most parasitized skate species are the vulnerable *L. fullonica* and the near-threatened *R. microocellata* and *R. undulata*, which are among those with the most concerning status in Europe (IUCN 2024, <https://www.iucnredlist.org>). For these three species compared to the four others (the near-threatened *Raja brachyura* and *R. clavata*, and the least-concern *L. naevus* and *R. montagui*), the strong parasitic constraint both in terms of prevalences and abundances may contribute to accelerate their collapse. Therefore, parasite monitoring among skate populations is crucial, particularly for the most parasitized ones and for species with the most concerning status, such as *L. fullonica*, *R. microocellata*, and *R. undulata*.

5 | CONCLUSION

In the context of global change and worldwide decrease of biodiversity in marine ecosystems, a more comprehensive understanding of the complex interactions between metazoan parasites, elasmobranch hosts, and their environments appears crucial. The apparent low parasite diversity in skates from the English Channel and Celtic Sea, if corroborated by further extensive investigations, may be indicative of stressed ecosystems, as healthy ones are known to be rich in parasite species (e.g., Hudson et al., 2006; Marcogliese, 2005). Moreover, parasites may be considered as factors that influence the outcome of

predation and interspecific competition between sympatric species, which is expected to be detrimental to the most parasitized host species, potentially contributing to population decline, and then species collapse (Timi & Poulin, 2020). To take into account the parasitic factors is all the more important because IUCN status differs not only between species, but also for a given species depending on the geographic area (IUCN, 2024, <https://www.iucnredlist.org>). We strongly recommend incorporating parasitology in further research to improve the conservation and management of elasmobranchs and the preservation of marine ecosystems.

AUTHOR CONTRIBUTIONS

Claudia Gérard: Conceptualization, methodology, formal analysis, investigation, writing – original draft, review & editing, visualization. Caroline Trochard and Maxime R. Hervé: Formal analysis (statistical analysis). Héloïse Hamel: Investigation (fish dissections). Mélanie Gay: Investigation (DNA sequencing), review and editing. Michel Barbier: Investigation (DNA sequencing). Thomas Trancart: Funding acquisition, review and editing. Thomas Barreau: Resources, investigation (fish dissections), review and editing, funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

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